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THE OYSTER

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MANY facts about oysters seem stranger than fiction. For instance, a female oyster is known to produce upward of 100,000,000 eggs in a single season. The oysters in our bays, rivers and coves use more water in the course of their food gathering and their respiration and sanitation, than do the 135,000,000 persons who constitute the citizenry of America. This curious but prized mollusk spends part of its life as a free-swimming creature and then becomes sedentary. When it gives up its locomotion, it is not contented merely to lie on its back or stomach, but it skews over on its side and in this seemingly asymmetrical position may live the nine or ten years of its life. Though the animal may reach one foot in length, or may weigh 2½ pounds, its food is exclusively microscopic, much of which is smaller than common plankton material.

The oyster typically is a bottom dweller, but it will grow even more rapidly when suspended from the bottom and most rapidly at or near the surface. This animal is aquatic, yet it is not found in fresh water, nor is it present in great quantities in the open ocean. Though protected by a strong armor, it is especially susceptible to the depredations of star fishes and certain small snails. Our estimates of the number of germ cells produced during a season by a single male oyster reach the proportions of fantasy, sextillions and beyond. Eminent biologists have estimated that if all of the eggs from one grown oyster in a given season were to develop and their succeeding offspring were to survive through five generations, the resulting generation would, when grown, occupy a space equivalent to 250 times the volume of the earth. Thus the story goes. Perhaps Ripley should be paged.

History

Just when oysters became objects of economic interest is not known, but records of their being included in the human diet indicate that they were very commonly used and highly prized by the Romans. Pliny the Elder, 1900 years ago, told of their abundance in the Adriatic Sea, while Sallust, after his trip with Caesar to what is now England, said he could find only one good in the Britons: "They eat oysters".

The Aborigines of our own shores used oysters in vast quantities long before the white settlers found them drying this product for purposes of exchange with the interior tribes. Testimony as to the popularity of the oyster with the Indian is found in the many piles of shells, kitchen middens,

Figure 1. Semidiagrammatic Sketch of an Oyster (Dissected in left valve) a. Adductor muscle; b. Anterior end; c. Anus; d. Auricle; e. Anterior aorta; f. Dorsal aspect; g. Gills; h. Hinge ligament; i. Intestine; j. Liver; k. Mantle; l. Nerve; m. Mouth; n. Oesophagus; o. Palps; p. Pericardial cavity; q. Posterior aorta; r. Posterior end; s. Reproductive glands; t. Shell; u. Stomach; v. Tentacle; w. Ventricle; x. Ventral aspect.

that have been located around one-time camping grounds. Some of these piles contain tens of thousands of bushels of shells, which in late years have been mined for use in road building and for the manufacture of lime.

Economic Importance

The oyster fishery of the United States constitutes an industry of outstanding importance, while it is a paramount industry in the Chesapeake Bay area, and especially in Maryland, where in all of its branches upward of 10,000 citizens are employed every year. Considering the workers and those dependent upon them, the contribution of the oyster industry to the welfare of the citizens of Maryland is most impressive. The fact that the one-time level of abundance, an annual yield of 15,000,000 bushels, has dwindled to a level of production now under 3,000,000 bushels annually, gives reason for concern over the socio-economic outlook of the tidewater areas in the State. It should be pointed out at the start that there is perhaps no crop gathered from the ocean that is as susceptible as the oyster to culture methods. The decline in yields cited has resulted from lack of interest on the part of the economic and the educational leadership to overcome political prejudice and the very *mores* of the watermen themselves.

Since the oyster, in one species or another, is distributed pretty much world-wide, and since its biology and the economy of the harvests are much the same wherever oysters are found, this treatise will be limited to the East Coast oyster, *Ostrea virginica* Gmelin. Moreover, since the Chesapeake Bay from the first has been the area of greatest production, the conditions of that area will be stressed herein.

No doubt the reader will ask forthwith, "What is the Chesapeake anyway that it makes possible the great volume of food and the production of wealth, actual and potential, cited?" Production of 15,000,000 bushels of oysters in a single year, 1883, by about one-half, i.e. Maryland's part, of this body of water is stupendous. The magnitude of this yield becomes spectacular, especially when compared, in more familiar terms, with some of the commoner foods, say beef. From 15,000,000 bushels of oysters, approximately the same number of gallons of solid food matter may be shucked for the market. Using eight pounds as the weight of a gallon of solid oyster meat, we have 120,000,000 pounds. If we divide this total by 600 pounds, the weight of a dressed steer, we find the equivalent in pounds of 200,000 steers—not "longhorns", but the improved beef types. In other words, Maryland waters alone produce in pounds the equivalent of more beef, and these figures are for all types of cuts and even the scruffy, bony parts, than the entire yields of steers from New Jersey, Delaware, Maryland and West Virginia.

The Chesapeake Bay is one of the greatest natural culture mediums known to man, not alone because of its size, but because of the nutrient materials common to that body of water. One may think of it as one

thinks of the Nile River, where the water periodically overflows the banks and spreads over vast valleys to drop its supplies of detritus and rich material, dissolved and undissolved, which, upon return of the river's flow to normal, is left broadcast to increase the fertility of the soil. In just such a fashion as this, cyclic excesses of rich, run-off water, did the region in question establish itself as the "granary of the world" among the Ancients and, in turn, attract the "Wandering Children" of biblical times, or, more recently, help to incite a war, the effect of which on natural resources and on human society cannot even yet be evaluated. The Chesapeake Bay receives water from much of New York and Delaware, practically all of Pennsylvania and Virginia, all of Maryland, with smaller contributions from North Carolina and West Virginia, a vast and rich territory which constantly, not periodically, is sending inponderable tons of enriching matter to this reservoir for storage and consequent use in biological cycles.

Biology of the Oyster

Contrary to the opinion generally held, the oyster is a highly evolved form having, as it does, well-developed systems for digestion, circulation, respiration, response to stimuli, and reproduction. It is indigenous over a wide range of territory extending from the Gulf of St. Lawrence to the Gulf of Mexico, as far down as Vera Cruz. The most productive areas in this wide range of distribution are the estuarine bodies from Rhode Island to Texas, the Chesapeake Bay being by far the most productive region.

The oyster is highly specialized to gather the micro-organisms which constitute its food. As water is passed over the gills (Figure 1), four fringe-like appendages on the ventral and posterior surfaces, cilia gather the food particles. Secretion from the gills entangle these organisms and they are rolled into small balls or food masses and passed forward to the palps, or lips, in the immediate region of the mouth. In the course of this gathering and transportation of the food to the mouth, particles not acceptable as food, such as large plancters and detritus, are separated out and discarded. The action of the cilia serves at once the purpose of food gathering, and by the circulation of water over the gills, respiration and the removal of excretory and fecal matter. Obviously an organ which pumps water, collects and transports food, secretes, excretes and functions in respiration, is complicated. Oyster gills do all of these things effectively.

Food enters the mouth, which is located near the hinge of the shells, that is, anteriorly. From the mouth it is led to the stomach, a comparatively spacious organ, through a short tube, the esophagus. Digestive juices secreted by the folds of the stomach and by a massive gland, usually very dark in color and known as the liver, which surrounds the stomach, are discharged into the digestive tract. Aided by the crystalline style, a uniquely constructed amber colored and rather eel-shaped body that, un-

attached in the system, disappears some minutes after oysters are removed from the water, these juices break down and digest the food for diffusion and distribution throughout the body. Digestion is completed and absorption takes place for the most part in the intestine, a long tube (Figure 1) which runs posteriorly and ventrally to a point opposite the heavy muscle (adductor), whence it bends back upon itself, passing anteriorly and dorsally around the stomach, by the esophagus, and again posteriorly to an external orifice, the anus, located on the dorsal surface above the posterior edge of the adductor muscle.

The circulatory system takes the digested foods from the enteric canal and delivers them to the tissues over the entire animal. This system is not a closed one, as in the higher forms, but is comparatively well developed. It has a central pumping body, or heart, divided into auricle and ventricle regions. The direction of the flow of blood is regulated by a valve between the ventricle and the auricle. The heart lies in a cavity just in front of the adductor muscle. This, the pericardial cavity, is covered laterally by a thin membrane through which the strong pulsation of the heart may be seen in a living specimen, even after the severe shock of "opening" the oyster. Pulsation may continue, under favorable conditions of humidity and temperature, for hours after a valve has been removed.

Pulsation of the heart forces the aerated blood, a slightly gray, nearly clear fluid, from the auricle on into the ventricle, and from this chamber on through the arteries into the body parts, in which it passes over the digestive tract and gills before returning through the veins to the auricle. The blood passages between the arteries and veins are devoid of walls and are more in the nature of sinuses. Thus, the tissues are bathed in the food and oxygen-laden plasma, which, at the same time, takes up carbon dioxide to be discharged when the blood passes through the gills, thereby to effect respiration. As already indicated, great quantities of water are passed through the gills in the processes of gathering oxygen and the removal of waste matter.

Sense organs are not as highly developed in the oyster as might be expected considering the animal's sensitivity. In the anterior region, near the gullet, there is some centralization of nervous tissue from which nerve fibres run to all parts of the body. These tissues thicken in several regions, forming still smaller "ganglia" whose immediate connectives innervate the organs and the surfaces near them. On the margin of the mantle, the thick membrane that envelops the whole oyster, there project outward small tubercles or tentacles that are highly sensitive to touch. These bodies, normally extending out over the edges of the shells, receive impulses even of the most delicate nature, as a result of which the shells snap to upon the slightest provocation such as change of water pressure, density, rate of flow, and even change of light intensity. Such responses offer a high degree of protection for the soft-bodied animal. The tentacles

are usually highly pigmented, being darker by far than oyster gray. No eyes are found in adult oysters, though organs of sight are not uncommon in other species of mollusks.

Most noticeable in the organization of the oyster are the shells which, because of their concavity, offer ample space for the animal. These shells or valves are produced by the mantle, which, as previously indicated, is a heavy glandular membrane surrounding the oyster and which secretes a liquid substance that, upon hardening, becomes shell. Brooks, in his treatise, "The Oyster",[1] tells of his observations of shell building upon glass inserted within the valves, as follows: "At the end of twenty-four hours the glass was found to be covered by a transparent faintly brown film of thin gummy deposit, which exhibited no evidence of structure, and contained no visible particles of lime, although it effervesced when treated with acids, thus showing that it contained particles too small to be visible with a microscope. The gummy film is poured out from the wall of the mantle, and in forty-eight hours it forms a rough, leathery membrane fastening the glass over the inside of the shell. At about this time the invisible particles of lime begin to aggregate and to form little flat crystals, hexagonal in outline and about 1/2500 of an inch long. The crystals grow and unite into little bundles or groups, and new ones appear between the old ones, until at the end of six days the film has completely lost its leathery character and has become stony, from the great amount of lime present in it. In three or four weeks the glass cover is completely built into the shell and can no longer be seen, and its place is only to be traced by its form, which is perfectly preserved upon the inner surface of the shell. When broken out it is found to be coated with a thick plate of white shell, which is beautifully smooth and pearly upon the side nearest the glass. Microscopic examination of this plate shows that it is made up of an immense number of minute crystals, packed and crowded together into a solid mass, without any regular arrangement. These observations show that the new layers are thrown off in the form of a gummy secretion from the mantle, with the lime in solution, and that the particles unite with each other and form crystals while the gum is hardening."

Since lime is deposited in successive films (Figure 2) on the inside of the shells, it would seem that the space occupied by the oyster would eventually be filled to the exclusion of the oyster's body. However, this is not the case, for the mantle, when expanded, overhangs the edges of the concave shells and secretions are deposited thereon. Thus constantly the shells are being opened as their edges grow apace.

The hinge mechanism consists of a ligament (Figure 1) secreted by the anterior portion of the mantle. As in the case of shell, this is not living tissue in the common sense of the word. Binding the two shells together

1 The Oyster, 1905. Brooks, W. K., Johns Hopkins Press.

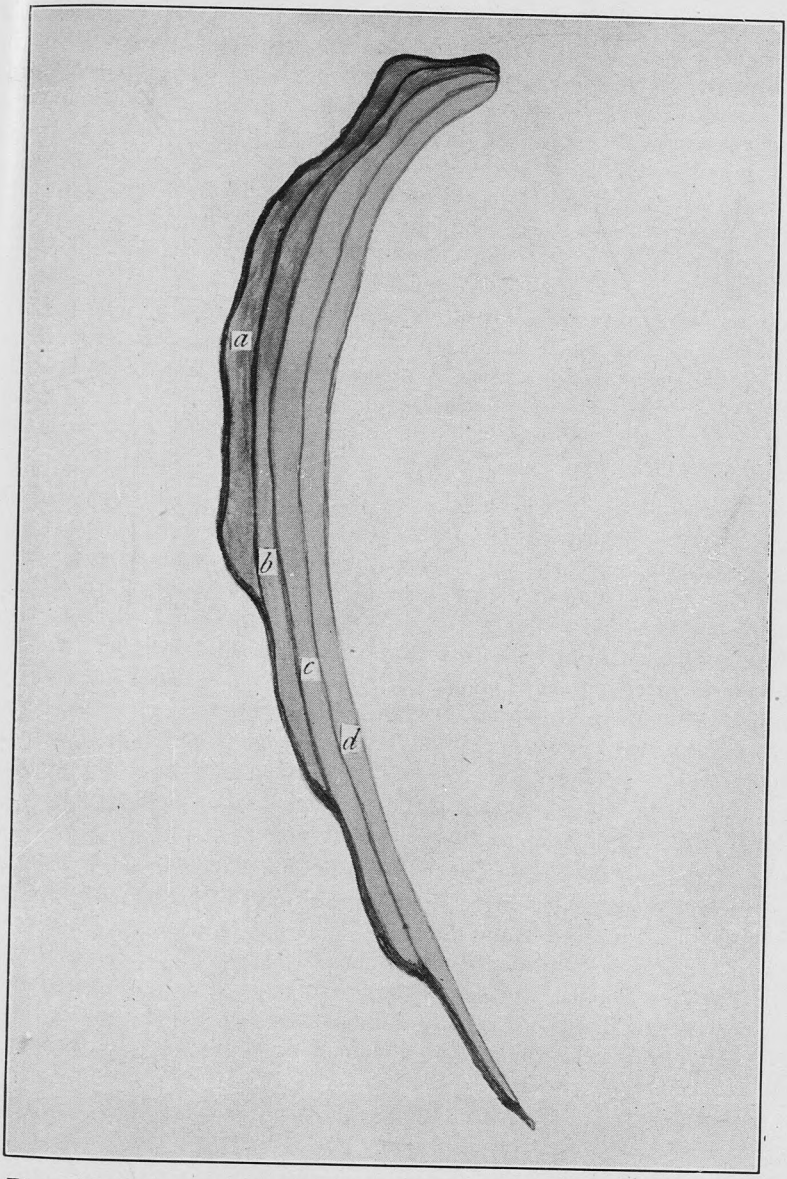

Figure 2. Diagrammatic Sketch of Longitudinal Section of a Shell From a Four-Year-Old Oyster, Showing Annual Deposits of Lime. a. First year; b. Second year; c. Third year; d. Fourth year.

it, at the same time, acts as a spring to force open the free ends of the shells. Since this ligament is not living substance and acts not only to hinge the shells, but to keep their free ends apart as well, it is apparent that the shells of an oyster would remain open indefinitely were not provision made for closing them. By means of the adductor muscle, a prominent and toughened mass of tissue just back of the heart, the shells may be closed tightly and strongly. It is this muscle that must be cut in the operation of oyster shucking. After it is severed, or upon death of the oyster, the shells open forthwith due to the hinge ligament. The adductor muscle is attached to the shells at points where the greatest mechanical advantage is derived and, as the shells are extended in growth, the muscle attachments grow outward to retain the relative mechanical advantage. The outward movement of the muscle is accomplished by an extension of the posterior section followed by absorption of the more anterior part. By breaking either shell lengthwise the progress of the outward migration of the muscle may be noted from the imbedded scar, or pinkish area, caused by the muscle imprint in the earlier stages.

Oysters in their native state keep their shells open nearly all the time, though frequently they are closed for protection and to wash out foreign matter, excretion, and fecal wastes. It is commonly held by watermen that an oyster opens its shell, feeds, and is active only on flood tide, but observations have established that the shells are opened on both flood and ebb tides, at night as well as during the day, and that they stay open upward of three-fourths of the time. However, the activity of the gills in respiration and feeding varies with the temperature and, as would be expected, lower thermometric readings tend to slow up activity. It has been shown that at a temperature of 4° C., or below, oysters cease to feed.[2]

Out of the water, oysters live for varying periods depending upon temperature and humidity. They may be kept long periods at very low temperatures, while, conversely, they die within a few hours if the temperatures are extremely high. The animal does not cease its vital activities when removed from the shell, and may remain alive for many hours, the length of time depending upon the physical conditions around it. The clear viscous fluid associated with shucked oysters of commerce is due to congealed blood and to substances secreted and thrown off by the oysters themselves and is not a sign of decay, as many purchasers of the raw commodity believe.

Eastern oysters have their sexes separate, differing thereby from the common European form, *Ostrea edulis,* each of which has two sex systems present in its body. The reproductive system, whether male or female, is located in the more bulky portion of the animal. Without the aid of a microscope the sex of an oyster cannot be told, although, when "ripe", a

2 Paul S. Galtsoff, 1928. Experimental Study of the Function of the Oyster Gills and Its Bearing on the Problem of Oyster Culture and Sanitary Control of the Oyster Industry. Document No. 1035, U. S. Bur. Fish.

greater part of the reproductive system is plainly visible to the unaided eyes, due to the distention caused by the vast number of germ cells present or in the course of maturation. In this distended condition the reproductive system has somewhat the appearance of a tree, with the base of its trunk opening to the exterior in the region of the pericardium and its branches anastomosing to the extent of covering nearly the entire lateral surface, there being an organ on each side of the oyster body.

Oysters eject their reproductive cells (Figure 3) directly into the open waters where, if the sperms and ova chance to come in contact with each other, fertilization ensues. The ejection of female cells is accompanied, or, possibly, aided by sudden snapping of the valves which forces the water,

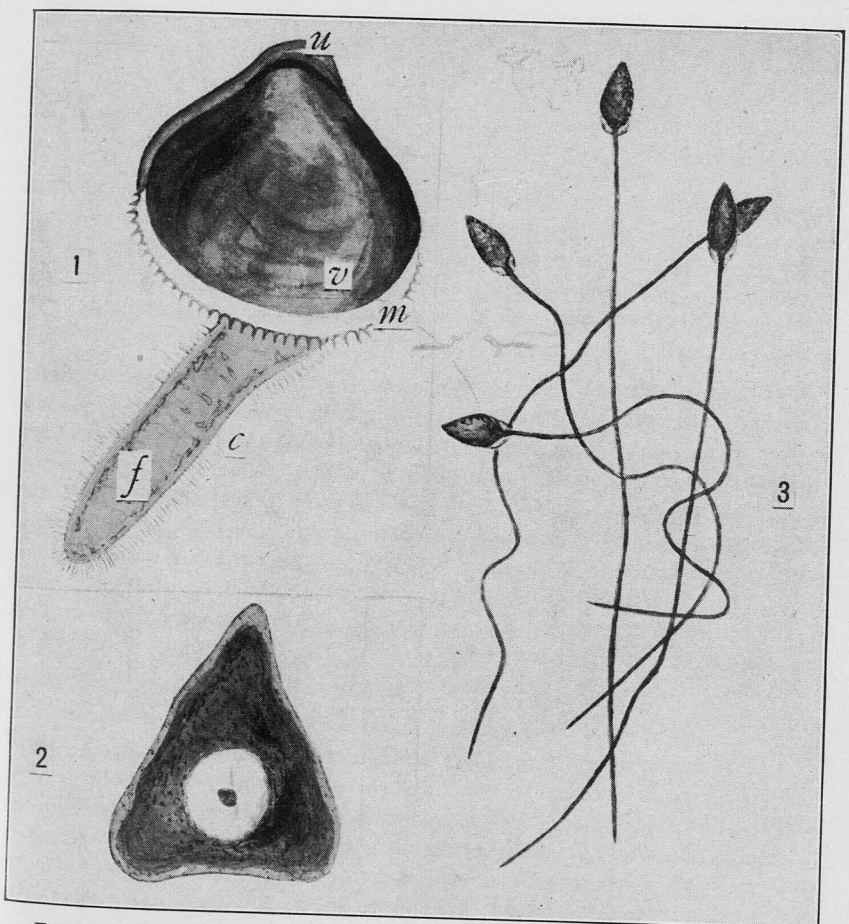

Figure 3. Fully Developed Oyster Larva, magnified 160x. 1.c. Cilia; f. Foot, m. Mantle, u. Umbo, v. Shell or valve. 2. Egg of Oyster magnified 550x. 3. Male Cells of Oyster, enlarged 2000x.

loaded with cells, from around the body of the oyster and out into the open waters. At short intervals this operation is repeated, each time a small cloud, nearly cream colored, being produced, so abundant are the cells. Male cells are emitted without shell snapping. It has been estimated at the Chesapeake Biological Laboratory that a single female contained 49,000,000 eggs—a very conservative estimate—while, in the male, the germ cells may be present, to repeat, in such prodigious numbers as to baffle ordinary methods of computation, millions upon millions of them being found. In a small oyster whose gonads were not extraordinarily distended some 2,960,000,000 spermatozoa were estimated to be present. These figures on germ cells cover only those present at a given time and do not take into consideration the fact that there may be two or three major spawnings by an oyster with consequent much greater numbers of cells.

The oyster is, as previously indicated, dioecious. How true this statement is, however, depends upon the philosophic state of the mind for at several points in its range individuals of the species have been observed to change their sex, thus to have alternate sexes from year to year.

Oyster eggs taken from the ovary have somewhat the shape of a kernel of corn, but upon fertilization they become round. The male cell is roundish with a tail-like appendage which drives it through the water (Figure 3); spermatozoa being mobile, while ova are without the power of movement. Milt and spawn are interchangeable terms applied to the genital products.

There is a marked correlation between spawning activities of oysters and the temperature of the water. In the Chesapeake region and, for that matter, through the greater part of the habitat of the species, oysters begin to spawn freely when the temperature reaches about 20°C. Optimum spawning takes place at 24°C., while there is an almost complete cessation of spawning when the temperature of the water reaches 28°C. Oysters with ripe gonads can be excited to spawn if, taken from water ranging about 24°C., the temperature of the water around them is gradually raised to the optimum degree, or slightly above it, and germ cells from the opposite sex are added. Knowledge of facts about spawning contributes to a better understanding of the proper time to plant shells or other cultch in order to secure a maximum catch for farming purposes.

Developing oyster eggs lend themselves well to study since they are hardy, relatively clear and of a highly satisfactory size to be observed as proliferation of cells and tissue formation take place. Within four or five hours after fertilization, certain cells develop cilia by means of which an embryo rises from the bottom and swims about. Rapid changes occur as the organs develop and at 24 hours a microscopic larva is produced, a free-swimming, feeding, bivalved animal with a prominent foot and mantle (Figure 3). About 15 days time is required to complete larval growth at which time, and of the size of a fly speck, the young oyster seeks out a

clean, hard surface to which it attaches itself. Henceforth, it lives a sedentary life, depending upon the currents to bring to it food and oxygen and to carry away the waste materials.

"Setting" and "spat-fall" are synonymous terms applied to the act of oyster larva attachment, a seasonal development, while the recently attached individual is known as a "spat". With the foot protruded, a larva scuds across objects, seemingly to feel out their surfaces and ascertain their availability for spatting. As previously stated, of necessity the surface must be permanent, clean, hard, and smooth; otherwise so delicate an organism would be subjected to many unconquerable hazards. When a favorable spot is selected the larva forces its adhesive foot out full length, about .22 mm., and temporarily attaches its tip. Around this point as a centre it draws itself toward the attached foot, releases the end of the foot and attaches it elsewhere only to pull the body up to the tip of the foot again. Repeating this performance several times and describing circles of successively smaller radii in the course of the action, it finally comes to rest with the left valve against the object and inclined toward the opening of the valves. From a lobed gland (byssus) at the base of the foot, secretions are produced at this time which, aided by the mantle and the foot itself, are distributed in such a way as to cement, upon hardening, the oyster to the surface.[3] About one quarter of an hour is required for the whole operation. The rest of its life is spent at this point and its success, as measured in survival, growth and reproduction, largely is determined by the tides.

Not all clean, hard surfaces attract larval oysters alike. Experimental work with such materials as brick-bats, oyster shell, broken glass, chips of various kinds of wood, coal, slag, pebbles, and other things suspended in wire baskets, side by each, over a prolific bed of oysters near Solomons Island, produced varying results. Using all the materials in a clean state and at a time when fully grown oyster larvae were known to be abundant in the water, shells proved to be preferable to glass, slag, pebbles, brick-bat, or chips. Glass was second in favor. Brick-bats, slag, pebbles and chips followed in order of choice.

Oysters are marine creatures. They are found in waters of the open ocean and in those of the upper estuaries or, in other words, they are distributed through saline waters ranging in salinity from [redacted]35 down to [redacted]5. The most intensive and extensive beds, however, are found in estuarine bodies whose richness in nutrients, no doubt, plays a big part in production. However, in salinities below [redacted]15 the major oyster enemies Screwborer (*Urosalpinx cinereus*) and the Star-fish (*Asterias forbesi*), are not able to survive, a fact of great importance to oyster farmers. In many regions, such as the seaside waters of Maryland and Virginia, these

[3] For further reference in connection with this interesting activity see The Attachment of Oyster Larvae, Biological Bulletin, Vol. XLVI, No. 3, March 1924, New Jersey, Thurlow C. Nelson.

pests destroy a major part of a crop annually and, under certain conditions, cause the loss of entire plantings, to the extent of hundreds of thousands of bushels of oysters. Under such conditions, natural beds do not exist. The distribution of salts in the vast Chesapeake Bay area, then, together with consequent distribution of enemies, accounts for the fact that in this area more oysters have been produced in a given year than from all other beds in the world put together.

Contrary to the position of many of America's natural resources, the oyster's future seems secure, since it is a hardy, highly fecund creature adapted to a wide range of chemical, physical and biological conditions and susceptible to cultivation and management. There is good reason to feel that it will not only continue the present yields, but that the future will find man utilizing the oyster in far greater abundance to recapture the nutrients washed from the land and stored in the brackish waters of the world, thereby to promote the advancement of the socio-economics of tidewater areas and the production of a commodity rich in vital food elements, the very elements in which our land crops from geologically old soil are so deficient.